true in the tadpoles where the operation had been successfully performed.

These experiments will certainly lead to a very extensive series of other investigations of similar kind. A large and extremely fruitful field of research is opened up by this work.

UNIVERSITY OF KANSAS, LAWRENCE.

THE RELATION BETWEEN THE GERM CELLS AND THE ENVIRONMENT.

BENNET M. ALLEN.

THE constitution of the germ plasm is one of the most prominent questions before biologists. This problem has been attacked by the study of cell lineage, deformation, mutilation and chemical treatment of eggs before and after fertilization; by a study of the relation between egg and sperm in fertilization, and through it all have run the brilliant developments in the field of cytology and experimental breeding. We have thus come to understand some of the cardinal facts regarding the mechanism of heredity.

The individuality of the chromosomes; their occurrence in pairs; the sex chromosomes; sex-linked characters; the fatal results of multipolar division; the explanation of mutations upon the basis of chromosomal defects and mixtures—all of these results have been interpreted to show that the potentialities of the germ plasm are laid down in the *physical* structure of the chromosomes. But through all this work we have difficulty in estimating fact and theory at their proper value. This has led to our elevating theories to the rank of established truths. Many have come to believe that the germ plasm is aloof from the soma and absolutely proof against any changes that may take place in the environment.

Without allowing ourselves to dogmatize upon this subject, let us inquire into the nature of the relation between the soma and the germ cells.

In studying the early history of the germ cells of the vertebrates, I have been struck by the fact that they undergo an orderly migration from analgen, that are often remote, toward the regions where the gonads will ultimately develop. They appear to be guided and stimulated by influences exerted by the body cells. This striking migration of the germ cells re-

sembles the movements of pigment cells, and suggests the collecting of leucocytes toward points of infection. While most of the somatic cells of the embryo are syncitial during these early stages, the germ cells show sharp contours, and by their migration they must certainly break any protoplasmic bridges that may have united them with surrounding cells. It is, however, quite possible that new protoplasmic bridges may be afterward established. Color is lent to such a view by the relation of the follicular cells to the ovum in many vertebrates. Whether this be true, or not, there are intimate chemical relations between the germ cells and the soma.

The rapidly multiplying male germ cells, and the ova, with their enormous increase in size, demand large amounts of nutriment. Various other substances in the blood are absorbed into these cells, as demonstrated by Riddle in his experiments of feeding Sudan III to hens. If we assume that slight changes in the chemical constitution of the germ plasm might modify its hereditary tendencies, then it would be easy to understand that many changes in the substances carried by the blood, such as foods, drugs, waste products, internal secretions, etc., must exert a decided influence, because we should expect them to modify so complex and unstable a substance as protoplasm.

Unfortunately, we know but little regarding the nature of the changes that these substances may produce in the germ plasm.

These are the *a priori* considerations. What are the facts?

Certain external influences are found to produce deleterious effects upon the germ cells. Bardeen subjected the germ cells of toads to the action of X-rays, and found that while the fertilized egg started to develop, the embryos produced became more and more abnormal. Similar effects have been produced by radium.

Stockards' experiments upon alcoholized guinea-pigs show that poisons not only affect the soma but the germ cells as well, and that the injuries are manifested in later generations in weakened, defective individuals.

These effects are of a gross general nature and do not touch the question of the more subtle changes that may be produced in the germ cells by the action of external influences.

The striking experiments of Tower upon *Leptinotarsa*, of Klebs upon *Sempervium*, of MacDougal upon *Oenothera* and

Raimannia, and of Gager upon *Onagra,* have shown that various external influences, chemical and physical, acting upon organisms, can produce specific mutational changes in the germ cells, and that these changes remain permanent through future generations.

From these permanent modifications we may pass to a class of changes that are less fixed; that may be strengthened by long subjection to these influences until they become more and more definitely and permanently transmitted to future generations. The rather incomplete experiments of Woltereck upon daphnians represent such cases.

In other cases these influences may not originate characters, but are merely capable of determining dominance of one over the other when they are nicely balanced. Some of Tower's experiments upon *Leptinotarsa* show this. Recent experiments in the modification of the reproductive processes of daphnians and rotifers likewise illustrate this principle.

There is some difference of opinion regarding the nature of these changes; but it appears to be very definitely shown in the rotifers that parthenogenetic reproduction can be maintained an abnormally long time by exerting certain stimuli—food (Nussbaum and Mitchell), waste products dissolved in the culture medium (Shull), etc. These measures prevent the development of male-producing females. It has been shown that these are really sexual females, which, if impregnated, produced winter eggs that develop into females. Morgan, Shull, Whitney and others have urged that these influences determine whether there should be a parthenogenetic or sexual phase of reproduction; but as Mitchell has pointed out, this is a change from a condition in which regular parthenogenetic (unfertilized) eggs produced females to one in which eggs capable of being fertilized produced males in the absence of fertilization.

While these external influences are very potent when the egg is susceptible, it has been shown that they cannot overcome certain internal factors that make for sexuality in cultures that have passed through many parthenogenetic generations.

Equally striking results were attained by Woltereck in daphnians. He found that meager feeding, and, indirectly, temperature, tend to produce sexuality in these forms.

We may also point to the experiments in sex determination among amphibians as carried out by Miss King and by Richard Hertwig and his students. One difficulty with amphibian material is the long delay in sexual differentiation in certain strains. These very conditions point strongly toward sexual indifference which manifests itself in the hermaphroditic tendency to be observed in the toad. Is it not possible that the primitive germ cells, at least in these cases, may be truly indifferent? The differentiation that appears later might be brought about by the action of delicately balanced internal and external factors. Color is lent to this view by the fact that in many forms the secondary sexual characters develop in response to stimuli coming from the gonads, even when germ cells are entirely lacking in the latter. Why should we consider the differences between ova and sperm to belong to a category apart from the "so-called" secondary sexual characters?

In the minds of many the problem of sex determination is practically settled in favor of the sex-chromosomes theory. There seems now little doubt that this applies quite widely, if not universally, among the insects. While the presence of sex chromosomes has been demonstrated in many other types of animals, and the union of a sex chromosome with one of the other chromosomes in *Ascaris* has suggested that it may thus escape observation in still other forms where it has not been demonstrated, the fact remains that there are many forms where it has been most diligently sought without success.

In organisms where the sex chromosome is clearly demonstrable in each somatic cell, we should suppose that it could influence its cell in each case toward its respective line of sexual differentiation. For this reason we need not feel surprised to find in the experiments of Kellogg, Harms, Messenheimer and Kopec upon lepidopterous larvæ the clearest demonstration that the secondary sex characters in those forms are wholly independent of any influence from the gonads. This is in sharp contrast to the experiments upon representatives of most of the other types of animals, notably the vertebrates, in which the gonads exert a profound influence upon the body as a whole.

It is not contended that the importance of the gonad as an organ of internal secretion in a given species proves the absence

of the sex chromosomes. Both may be essential factors in this connection, in varying degrees of relative importance.

In spite of the highly critical attitude maintained toward the question of modification of the germ cells through influences from the environment, so much good evidence is accumulating that we cannot ignore these cases nor cry them out of court. While we can readily see how external influences acting upon the germ cells may so modify them that the offspring will be in some way influenced, it is difficult to accept, without more convincing proof, the experiments designed to demonstrate that characters acquired by the soma are transmitted to the germ cells in such fashion as to produce similar modifications in the soma of the offspring.

The experiments of Brown-Sequard, Kammerer and others, by which it is claimed that modifications such as injuries, changed instincts, changed color patterns, etc., are transmitted to future generations, have been so interpreted. It is so difficult to conceive of the mechanism by which these changes in the soma could be transmitted to the germ cells that we should demand far better proof than has thus far been brought forward; yet above all things, while we should maintain an attitude of skepticism, we should be free from dogmatic intolerance toward any really creditable work along these lines.

Much needs to be done in tracing out the effect of the environment upon fecundity and periodicity in reproduction. To what extent are these results attributable to modification of the germ cells? To what extent may these changes be inherited? While we have some data upon these points, as, for instance, in the case of sheep, the field is large and much needs to be done in it.

Domestication of animals introduces a whole series of complex factors involving change of food, modifications of climate, protection from the weather, modification or loss of instincts, etc. These all exert a profound influence upon the reproduction of animals. It would be difficult in most cases to say in how far selection might also play a part. We know that in many failures to breed wild animals it plays no part. Little has been done since the time of Darwin upon these important subjects. Our attention has been so closely fixed upon the study of the mechanism of reproduction that we have largely

neglected these problems concerning the influences that may induce modifications in it.

I predict that the study of the relations between the germ cells and their environment will yield some of the most important results in future biological investigations.

UNIVERSITY OF KANSAS, LAWRENCE.